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Research Article

Ecological niche characterization and interspecific associations among invasive *Pomacea canaliculata* (Mollusca, Gastropoda) populations in Jianghan Plain, China

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Abstract

Pomacea canaliculata is a major invasive snail species in freshwater ecosystems in southern China. Population outbreaks of this species threaten zoobenthic community structure and food web stability. However, the competitive mechanisms of invasive mollusks in zoobenthos communities remain poorly understood. Previous studies have neither systematically assessed the niche relationship between invasive mollusks and native zoobenthos communities nor identified the environmental driving mechanisms. To explore the niche, interspecific relationships, and relationships with environmental factors of the invasive community in the Jianghan Plain, 45 sampling sites were established (15 each in paddy fields, ditches, and lakes). Zoobenthos were collected using Peterson mud samplers and D-shaped nets, alongside corresponding water samples. The analysis of the *P. canaliculata* invasive community primarily focused on the dominant zoobenthos, niche width, morpho-functional group, niche overlap, and connection coefficient. The survey results revealed 65 species of zoobenthos, among which arthropods were the dominant taxon, accounting for 69.2% (45 species), and functional feeding taxa were dominated by predators and scrapers. The niche width of *P. canaliculata* varied significantly across different habitats. In paddy fields, *P. canaliculata* occupied a medium niche; in ditches, a narrow niche; and in lakes, a broad niche. In paddy fields, the niche overlap between *P. canaliculata* and major zoobenthos was low, with no species pairs exhibiting $O_{ik} > 0.6$. In ditches, the niche overlap between *P. canaliculata* and major zoobenthos was relatively low, with only 28.57% of species pairs having $O_{ik} > 0.6$. In lakes, the niche overlap between *P. canaliculata* and major zoobenthos was high, with 66.67% of species pairs having $O_{ik} > 0.6$. The invasive community was positively associated overall ($VR = 1.51$, $W = 45.23$), and the species were relatively independent of one another. *P. canaliculata* was strongly associated with *Diplonychus* sp., *Micronecta* sp., *Anisops* sp., *Aciagrion* sp., *Caridina* sp., and *Macrobrachium* sp. According to environmental factor analyses, NH_3-N, chemical oxygen demand, total nitrogen, and water temperature are the main environmental factors affecting the distribution of *P. canaliculata*. Overall, the results showed that invasion by *P. canaliculata* can affect the community structure and food web relationship of the zoobenthic community; however, the specific consequences and extent of the invasion are restricted by many factors.

Key words: Biological invasion, community structure, interspecific connectivity, zoobenthos

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Introduction

Biological invasion refers to the phenomenon where organisms enter a new environment, survive, reproduce, and their populations further spread, causing harm to local ecosystems, economies, or even human health (Fan et al. 2013). Many human activities, such as agriculture, aquaculture, and transportation, have facilitated the intentional or unintentional spread of species across their natural dispersal barriers (Zhou et al. 2024). As international and regional exchanges and cooperation become more frequent, biological invasions have become a global issue (Liu et al. 2021a). Compared to terrestrial ecosystems, aquatic ecosystems have distinct boundaries, making them more susceptible to invasion by alien species, with freshwater ecosystems being particularly affected (Chen 2010). The Jianghan Plain in south-central Hubei Province, China, is a typical wetland ecosystem in the middle and lower reaches of the Yangtze River (Li et al. 2003). Its dense river network system supports rich biodiversity and is a key food production base. Despite its ecological and economic importance, the aquatic ecosystem in this region is facing serious threats, including biological invasion (Ouyang et al. 2004). *Pomacea canaliculata* is one of the typical examples of biological invasion in the Jianghan Plain. It is native to the Amazon River basin, was introduced to China in 1981, and has greatly expanded owing to its predatory nature, strong fecundity, and environmental tolerance (Guo and Zhang 2014). This species is seriously threatening the structure and ecological function of the community (Liu et al. 2021a).

Research on the impacts and mechanisms underlying biological invasion typically explores two key aspects: the effects of invasive species on communities, and how resident species respond via alterations to their niches and interactions (Jiang et al. 2019; Guo et al. 2021; Wang et al. 2022; Ji et al. 2023). Ecological niche theory provides an effective framework for analyzing the competitive advantages of invasive species (Zhang 2018), characterizing resource-utilization capacity through niche width, niche overlap reflecting interspecific competition intensity (Guo et al. 2022), and interspecific associations (Xu et al. 2016). These are used to explore biological relationships and understand interspecific relationships, structure, species diversity, population evolution, and dynamic succession (Deng et al. 2018). Niche theory and interspecific connectivity methods have been widely applied to birds (Dong 2013), plants (Zhou et al. 2024), plankton (Huo et al. 2024), macrobenthos (Shi et al. 2023), and swimmer communities (Li et al. 2017). However, a considerable research gap remains regarding the competitive mechanisms of invasive mollusks, such as *P. canaliculata*, in zoobenthos communities. As key functional groups in aquatic ecosystems, zoobenthos are drivers of material cycling and sensitive indicators of environmental change (Xu et al. 2021), and their community dynamics directly affect ecosystem stability (Wang et al. 2022). Previous studies have mostly focused on invasion hazards (Wang et al. 2021), potential geographic distribution (Zhang et al. 2016), bioecological characteristics (Yang et al. 2016), and response to a single environmental factor (Zhu et al. 2015), but to our knowledge, have not yet systematically assessed their niche relationship with native zoobenthos communities, and the environmental driving mechanism involved remains unclear.

Studies on the effects of environmental factors such as high and low temperatures, drought, and salinity on *P. canaliculata* have provided a scientific basis for developing more effective control strategies (Guo and Zhang 2014; Zhu et al.

2015; Yang et al. 2022). The growth dynamics and density changes in *P. canaliculata* are significantly influenced by various environmental factors, such as food, habitat, and temperature (Yamanishi et al. 2012). In Hong Kong, China, *P. canaliculata* density is higher in water bodies with higher phosphate and alkalinity levels (Kwong et al. 2008). In some rivers of Buenos Aires Province, Argentina, the physical and chemical properties of the water and vegetation jointly influence *P. canaliculata* abundance (Seuffert and Martín 2013). In the Chikugogawa River basin in Kyushu, Japan, the density of *P. canaliculata* shows a significant negative correlation with predators such as crustaceans, dragonfly larvae, carp, and turtles (Hara et al. 2015). In Japanese rivers, biological factors are determinants of *P. canaliculata* density, whereas dissolved oxygen has not shown a significant effect on density (Yamanishi et al. 2012). Additionally, pH affects the survival and physiological activities of *P. canaliculata* (Zhu et al. 2015). The biomass of *P. canaliculata* in the Florida Everglades in the United States increases with rising pH levels (Pierre et al. 2017). These observations suggest that *P. canaliculata* may have a broader tolerance range for various environmental factors associated with water, which could be a reason for their successful invasion.

The aim of this study was to investigate the following three scientific questions: (1) the niche width and overlap characteristics of the main zoobenthos in a *P. canaliculata* invasion community; (2) the interspecific relationships and mutual influences between *P. canaliculata* and the main zoobenthos; and (3) the main environmental factors affecting the distribution of *P. canaliculata* invasions.

Study area

The Jianghan Plain is in central-southern Hubei Province (29°26'–31°12'N, 111°45'–114°5'E), covering an area of approximately 47,000 km^2 (Cai and Luo 2015). It primarily encompasses eight counties and districts under the jurisdiction of Jingzhou City, as well as three provincial-level cities directly administered by the province (Qianjiang, Tianmen, and Xiantao), and extends to parts of five prefecture-level cities (Wuhan, Yichang, Jingmen, Xiangyang, and Yichang) (Wang 2024). The Jianghan Plain has a subtropical monsoon climate, characterized by distinct seasons, with cold and dry winters and hot, humid summers with abundant rainfall. The annual average temperature is approximately 17 °C (Chang et al. 2023) and the annual average precipitation is 1,100–1,300 mm, with approximately 70% of the total precipitation occurring between April and July (Ma 2023). The Jianghan Plain has a low-lying terrain with an average elevation of approximately 27 m, and the terrain slopes gently from northwest to southeast (Fan 2024). The region is rich in rivers and lakes, forming a network of waterways that provide habitats for various plants and animals. Common plants include *Oryza sativa*, *Zizania latifolia*, *Phragmites australis*, *Trapa bispinosa*, *Nelumbo nucifera*, *Gossypium hirsutum*, *Triticum aestivum*, and *Brassica napus*. Common animals include *Carassius auratus*, *Hypophthalmichthys molitrix*, *Monopterus albus*, *Pelteobagrus fulvidraco*, *Egretta garzetta*, *Anas zonorhyncha*, *Pelophylax nigromaculatus*, and *Pelodiscus sinensis* (Ma 2023).

Owing to suitable natural conditions such as average annual temperature and annual precipitation, *P. canaliculata* has rapidly spread and proliferated after invading the Jianghan Plain, posing a serious threat to the stability of agricultural ecosystems (Liu et al. 2020). Between 2001 and 2010, the

development of the shrimp-rice co-cultivation farming model increased water connectivity, resulting in an upward trend in the invasion and spread of *P. canaliculata* (Ni et al. 2022). Since 2010, *P. canaliculata* has spread widely across the Jianghan Plain, including in the cities of Jianli, Jiangling, Honghu, Shishou, Gong'an, Xiantao, Tianmen, and Qianjiang, inhabiting wet habitats such as paddy fields, ditches, and lakes (Liu et al. 2020).

Sampling efforts

In 2022 and 2023, *P. canaliculata* surveys were carried out in Hubei Province, China. The line trekking method was used to investigate the distribution of the snail. The locations, latitudes, longitudes, and altitudes of the sites were recorded, and the area of occurrence was investigated in detail to obtain preliminary results of the distribution and hazard status of this species (Suppl. material 1). Based on the identification of the hotspot distribution areas of *P. canaliculata* (> 10 per m^2) in the early stages, we launched a benthic fauna survey in July–August 2024 (the peak season of aquatic life activity) in the Jianghan Plain, with 15 sampling points each in paddy fields, ditches, and lakes, for a total of 45 sampling points (Fig. 1).

Materials and methods

Collection and identification of samples

Sample collection and processing

Paddy fields were continuously trawled with D-shaped nets (20 cm wide, 420 μm aperture) for 2 m along the ridge-water interface (Ministry of Ecology and Environment of the People's Republic of China MEE 2023). Ditches and lakes were sampled with 1/16 m^2 Petersen's mud collectors to collect the surface substrate of undisturbed zones (≤ 2 cm in depth). All sample points were set up with three parallel sample squares (China National Environmental Monitoring Centre 2021). After filtering and rinsing the sample through a 0.3 mm sieve silk grading, the remaining portion was placed in a white enamel dissection tray. Zoobenthos organisms were picked out one by one with tweezers and quickly placed in 75% ethanol for fixation.

Species identification and functional grouping

Zoobenthos samples were identified to the species/genus level by taxonomists from the Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan, China. Based on the delineation rules of Cummins (1974), Barbour et al. (1999), and Ode (2003), zoobenthos samples were categorized into the following five functional groups: collectors that feed on various organic debris (particle size < 0.45 mm) at the water bottom; filter feeders that feed on fine suspended organic particles (particle size < 0.45 mm < 1 mm); scrapers that feed on various organisms that live in the solid state; predators that feed on other aquatic animals; and shredders that decompose various types of apoptotic and coarse organic matter particles (particle size > 1 mm).

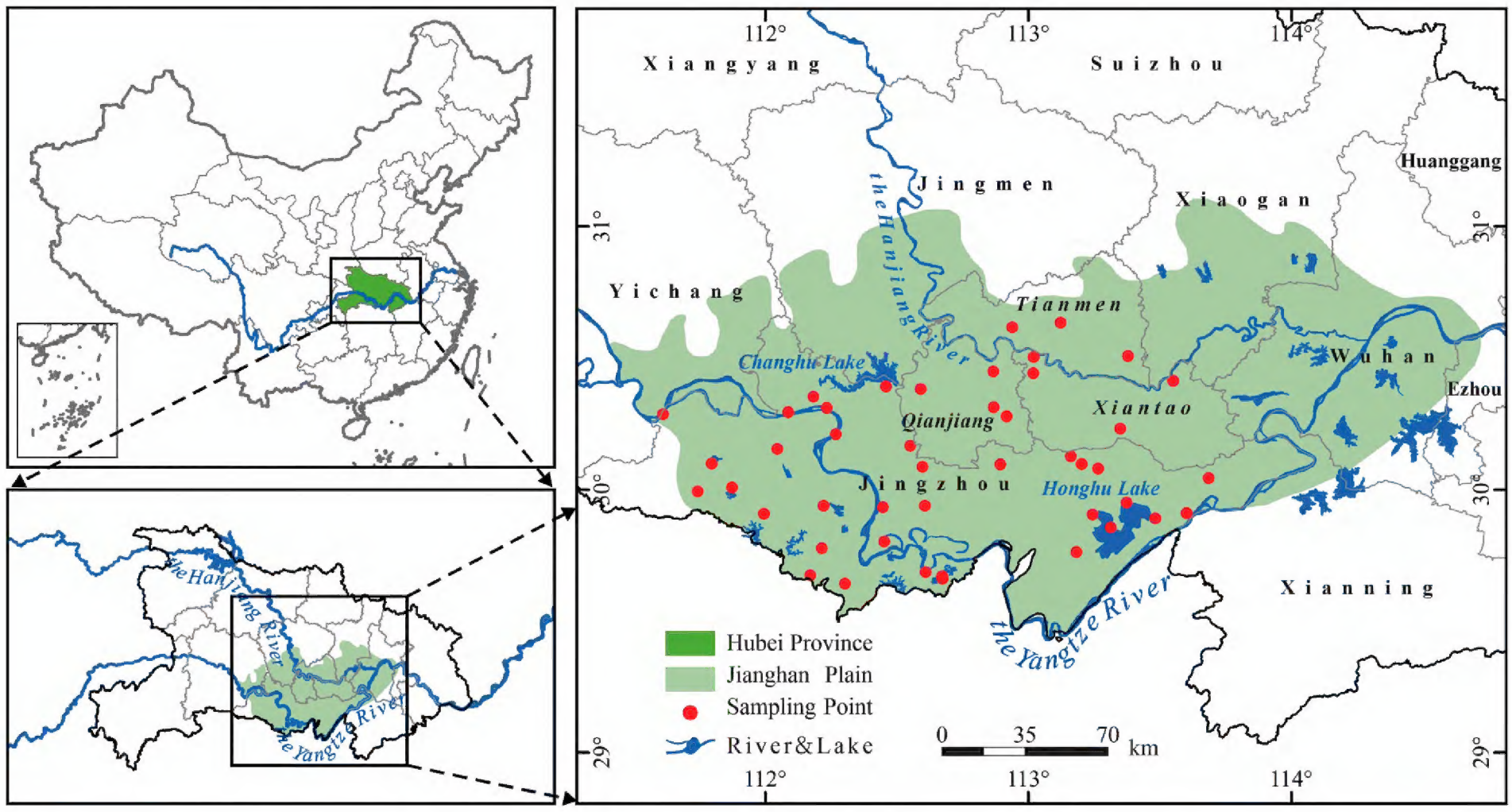

Figure 1. Schematic diagram of sampling sites in the Jianghan Plain.

Determination of environmental factors

When collecting zoobenthos samples, the YSI portable water quality analyzer (YSI 6680, Yellow Springs Instrument Co., Yellow Springs, OH, USA) was used to simultaneously determine the water temperature (WT), DO, electrical conductivity (EC), and pH. Water samples were collected from the surface layer using a 1 L water sampler, fixed with acid, stored at low temperature, and brought back to the laboratory on the same day to measure chemical parameters. Standard methods were then used to determine total N (TN), total P (TP), K, ammonia N (NH_3-N), chemical oxygen demand (COD), permanganate index (CODMn), and the average value of three parallel measurements according to the Water and Wastewater Detection and Analysis Methods (Wei 2002). All water samples were tested three times, and the average value was taken (Wei 2002). The three-dimensional coordinates of the sample points were recorded using a handheld GPS instrument (Garmin GPS-67, Nanjing Huantian Precision Instrument Co., LTD., Nanjing, China).

Data analytics

Dominance and diversity index

Dominance is the primary quantitative indicator for studying the relationships between species, reflecting the status and importance of species within a community. The McNaughton dominance index (Y_i) was used to assess the dominance of species in the zoobenthos (Lampitt et al. 1993); the Shannon diversity (H), Margalef richness (D), and Pielou evenness (J) indices were used to analyze the α diversity of the invasive community. The Jaccard dissimilarity index was used to measure the total β diversity of the community. The formulae are presented in Suppl. material 2.

Ecological niche characteristics

Niche width reflects the extent to which a species utilizes resources. The higher the value, the stronger the species' adaptability to the environment (Gleason 1926). The modified Levins' formula was used to calculate niche width (B_i) (Levins 1968). Niche overlap reflects the degree of similarity between species in terms of resource utilization or environmental adaptation. The greater the overlap, the greater the competition between species (Zhang 2018). The Pianka index formula was used to determine the niche overlap index (O_{ik}) (Pianka 1973) (see Suppl. material 2).

Overall connectivity analysis

The overall relatedness of the dominant species in the invasive community was determined based on the Schluter's variance ratio (*VR*) method (Schluter 1984), which reflects the degree of stability of the structure of the invasive community and the trend in succession. The statistic *W* was used to reflect the degree to which the *VR* deviated from 1 (Zhang 2018). The formula is presented in Suppl. material 2.

Determination of the degree of interspecific relatedness

A chi-square test (X^2) was used to conduct a qualitative study on the interspecific connectivity of the invasive community in the Jianghan Plain. Dominant species from each habitat were selected for interspecific connectivity and correlation analysis. A 2 × 2 contingency table was constructed between species pairs, and statistics were calculated for a, b, c, and d (Guo et al. 1997). The X^2 values were calculated using Yates' continuous correction formula for chi-square test (Zhang 1995).

The X^2 value cannot quantitatively differentiate the linkage strength (Zhang 2018). Therefore, it is necessary to further analyze the degree of interspecific connectivity using indices such as the coupling coefficient (*AC*) (Li et al. 2007), the Jaccard index (*JD*) (Li et al. 2023), and point correlation coefficient (Φ) (Lin et al. 2023). Additionally, the Spearman rank correlation test was used to reflect the correlation and closeness between species in the invasive community, thereby enhancing the reliability of the results (Bishara and Hittner 2012; Xu et al. 2016; Wu et al. 2025). The formulae are presented in Suppl. material 2.

Mantel test and redundancy analysis

The relationship between zoobenthos and environmental factors is complex. To clarify the contribution of each environmental factor, Mantel correlation analysis and redundancy analysis (RDA) were used to analyze the impact of each environmental factor on *P. canaliculata* invasion. Using DO, COD, BOD, WT, NH_3-N, TP, TN, CODMn, EC, and K as matrix factors, the Mantel's test was employed to analyze the correlation between zoobenthos biomass and the environmental factor matrix, thereby identifying the primary influencing factors affecting the distribution of benthic animal communities invaded by *P. canaliculata* (Somers and Jackson 2022). To eliminate the impact of data variability and ensure equal treatment of each feature dimension, all data were standardized via square root transformation prior to analysis. RSTUDIO software was used to plot results of

the Mantel's test (Li et al. 2024). Thresholds were set as follows: $r < 0.2$ indicated weak correlation; $0.2 \leq r < 0.4$ indicated relatively high overlap and moderately small closure; $r \geq 0.4$ indicated that the two matrices mostly overlapped with the highest degree of overlap (Chen et al. 2024).

As rare species have a significant impact on the ranking results, we selected the biomass of dominant species in three habitats and environmental factors for the ranking analysis (Muylaert et al. 2000). CANOCO 5.0 software was used to perform detrended correspondence analysis on the species richness matrix. The maximum length gradient values in the first four axes of the detrended correspondence analysis ranking were greater than 3. Redundancy analysis was then conducted. Significant environmental factors ($P < 0.05$) were screened using forward selection and Monte Carlo tests (499 iterations) to explore the impact of environmental factors on species distribution.

Sampling sites were mapped using ARCGIS MAP 10.6. The *McNaughton* dominance index, Levins' niche width index, and Pinaka niche overlap value were calculated using Microsoft EXCEL 2016, and the interspecific associations and Spearman's rank tests were calculated using the "spaa" package in the R 4.0.5 software (Zhang 2025). Mantel test correlation analyses were performed using the "vegan," "ggplot2," "ggrepel," and "ggcor" packages. Redundancy analysis was performed using CANOCO 5.0 software, and significance tests were performed using the Monte Carlo permutation test.

Results

Characterization of invasive community structure

Category composition

Sixty-five zoobenthos species were identified in the 45 sampling sites, belonging to 3 phyla, 5 classes, 11 orders, and 34 families. There were significant differences in the number of zoobenthos species across different taxonomic groups (Fig. 2A, Suppl. material 3). The phylum Arthropoda accounted for 22 families and 45 species, representing 70.8% of the total species (n = 65); the phylum Mollusca accounted for 9 families and 16 species, representing 24.6% of the total species; and the phylum Annelida accounted for 3 families and 3 species, representing 4.6% of the total species. The proportion of benthic invertebrates across different groups varied across the three different habitats: arthropods had the highest proportion in ditches (72.3%, n = 47), followed by paddy fields (68.8%, n = 45), and lakes (57.5%, n = 40); mollusks had the highest proportion in lakes (37.5%), followed by paddy fields (24.4%), and ditches (21.3%). The number of species and proportion of annelids varied little across the three different habitats.

The analysis of functional feeding taxa showed that predators significantly dominated in all three habitats (paddy fields 45.45%, ditches 45.65%, and lakes 41.03%), followed by scrapers, with filter feeders, collectors, and shredders accounting for lower proportions (Fig. 2B). Collectors had the lowest proportion in paddy fields (2.27%), whereas there were no collectors in ditches, where filter feeders had the highest proportion (17.39%). In lakes, both collectors and shredders had a proportion of 7.69%.

Current abundance and diversity

Zoobenthos species density in the three different habitats ranged from 440 to 3,496 ind./m^2, with an average of 1,406.15 ind./m^2 (Fig. 3A). The biomass ranged from 176.03 to 3,519.68 g/m^2, with an average of 1,452.72 g/m^2 (Fig. 3B). The average density in lakes (1,714.24 ind./m^2) was higher than that in ditches (1,420.51 ind./m^2) and paddy fields (1,114.32 ind./m^2), and the average biomass in lakes (2,434.98 g/m^2) was higher than that in ditches (1,003.03 g/m^2) and paddy fields (927.69 g/m^2). The results of the one-way ANOVA showed that the density and biomass of *P. canaliculata*-invaded zoobenthos communities differed significantly among habitats ($P < 0.05$).

The Shannon diversity index (H) for zoobenthos taxa in paddy fields ranged from 1.03 to 2.6, with an average of 1.6. The Margalef richness index (D) ranged from 0.87 to 3.36, with an average of 1.52. The Pielou index (J) ranged from 0.49 to 0.79, with an average of 0.66. The H for zoobenthos in ditches ranged from 1.29 to 2.32, with an average of 1.74. The D ranged from 1.81 to 2.37, with an

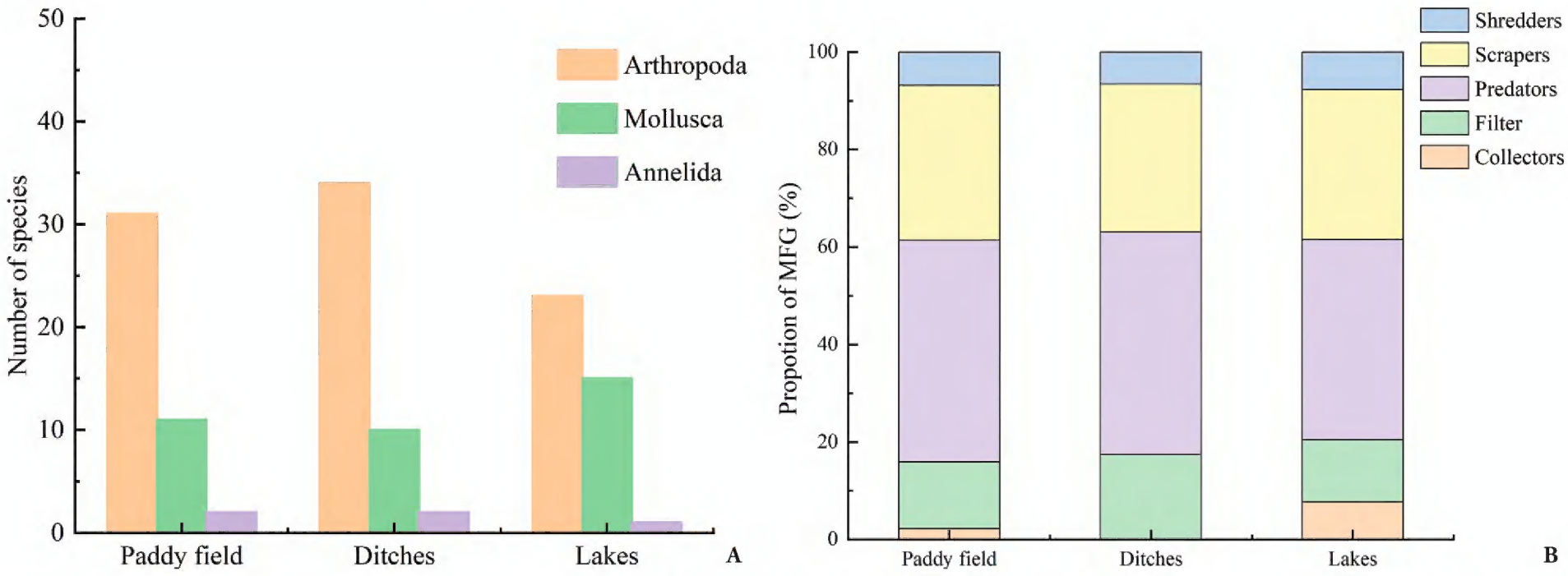

Figure 2. Dominant species in invasive communities and functional feeding taxa of zoobenthos. **A.** Composition of benthic fauna in paddy fields, ditches, and lakes; **B.** Classification of functional feeding groups of benthic animals in paddy fields, ditches, and lakes.

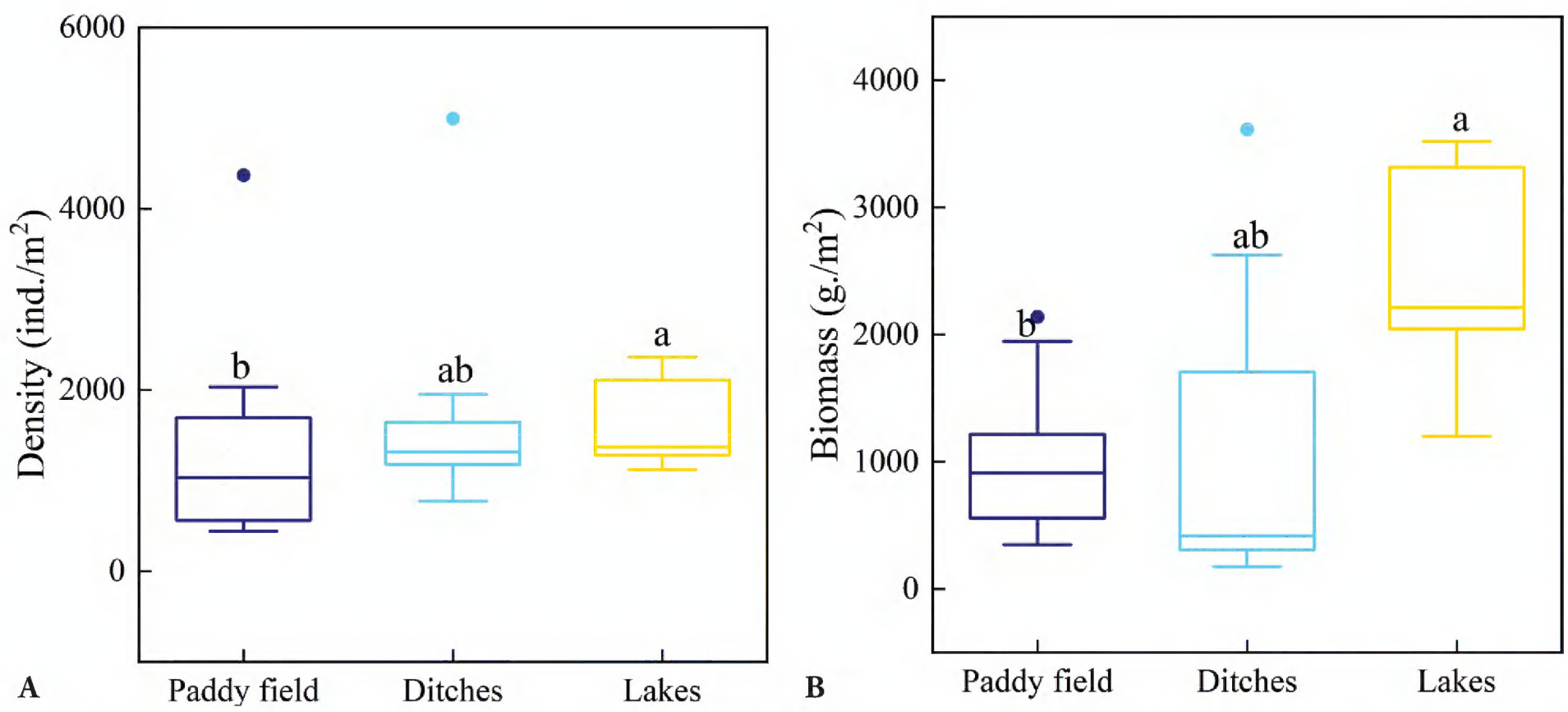

Figure 3. Density (**A**) and biomass (**B**) of the invasive *P. canaliculata* community in the Jianghan Plain. Different letters indicate significant differences ($P < 0.05$).

average of 1.64. The *J* ranged from 0.73 to 0.82, with an average of 0.69. The *H* for lakes ranged from 0.98 to 2.56, with an average of 1.54. The *D* ranged from 0.61 to 3.48, with an average of 1.56. The *J* ranged from 0.52 to 0.81, with an average of 0.62. The results of the one-way ANOVA showed that there were no significant differences in the *H*, *D*, and *J* among the three habitat types ($P > 0.05$) (Fig. 4).

The total β diversity of the invasive communities of *P. canaliculata* was 0.75 (paddy fields), 0.78 (ditches) and 0.85 (lakes), and was decomposed into replacement (turnover) components and richness difference (nested) components. According to the ternary phase diagram (Fig. 5), the replacement process contributed 67.80% (paddy field), 69.14% (ditch), and 48.46% (lake) to community β diversity, whereas the richness difference process contributed 32.20% (paddy field), 30.86% (ditch), and 51.64% (lake). Therefore, species turnover was the dominant process of variability in paddy fields and ditches, but nesting was the dominant process of variability in lakes.

Ecological niche of dominant species in invasive communities

Dominance

According to the calculation of dominance degree, there were 11 dominant species in the invaded community ($Y_i \geq 0.02$), including 7 in paddy fields, 8 in ditches, and 7 in lakes. *Pomacea canaliculata*, *Bellamya* spp., and *Diplonychus* spp. were distributed across different habitats (*fi* = 1). *Physa acuta*, *P. canaliculata* and *Bellamya* sp. were the dominant species ($Y \geq 0.1$) in paddy fields; *Aciagrion* sp., *P. acuta*, *P. canaliculata* and *Bellamya* sp. were the dominant species in ditches; *Caridina* sp., *Macrobrachium* sp., *P. canaliculata*, and *Bellamya* sp. were dominant in lakes.

Niche width of dominant species

According to the niche width, the dominant species were roughly divided into broad ($B_i > 0.70$), middle ($0.50 \leq B_i \leq 0.70$), and narrow ($B_i < 0.50$) niche species (Li et al. 2023). The niche widths of the dominant species are shown in Table 1. The niche widths of species in paddy fields ranged from 0.13 to 0.60.

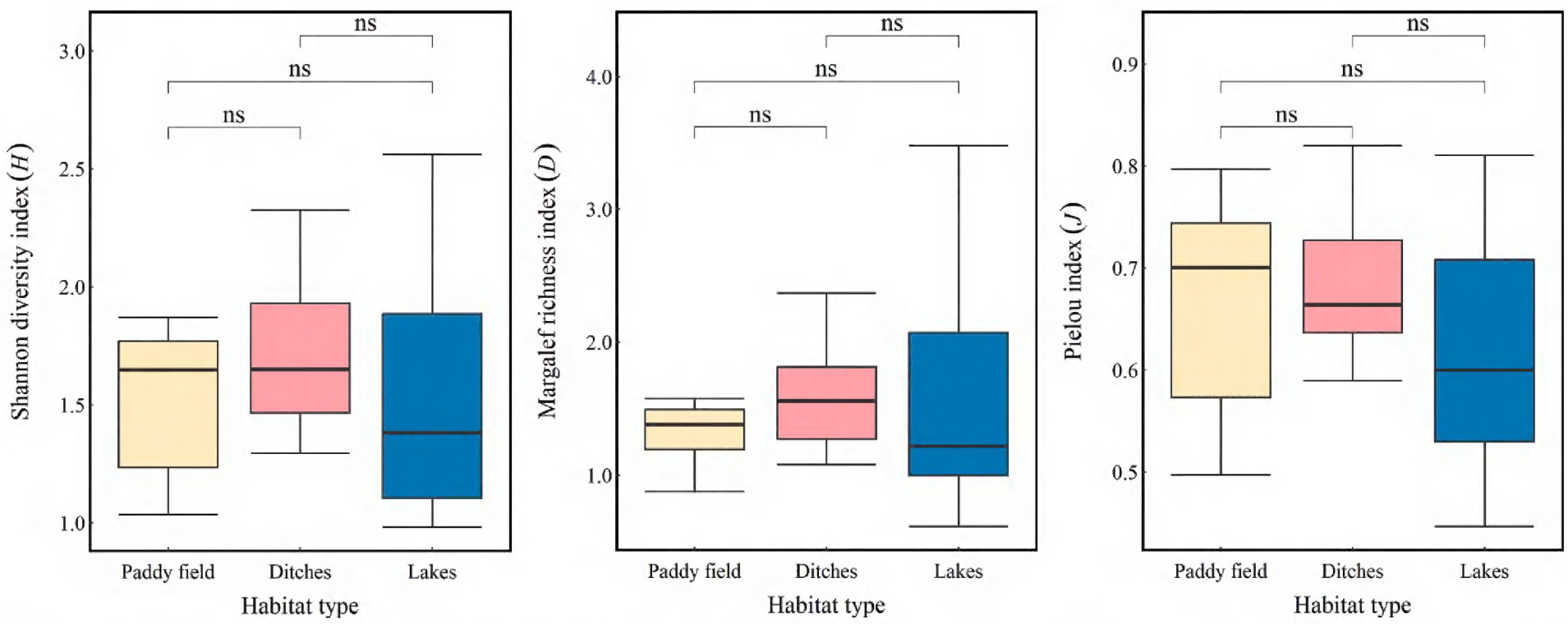

Figure 4. Shannon diversity (*H*), Marglef richness (*D*), and Pielou (*J*) indices of invasive *P. canaliculata* communities in the Jianghan Plain.

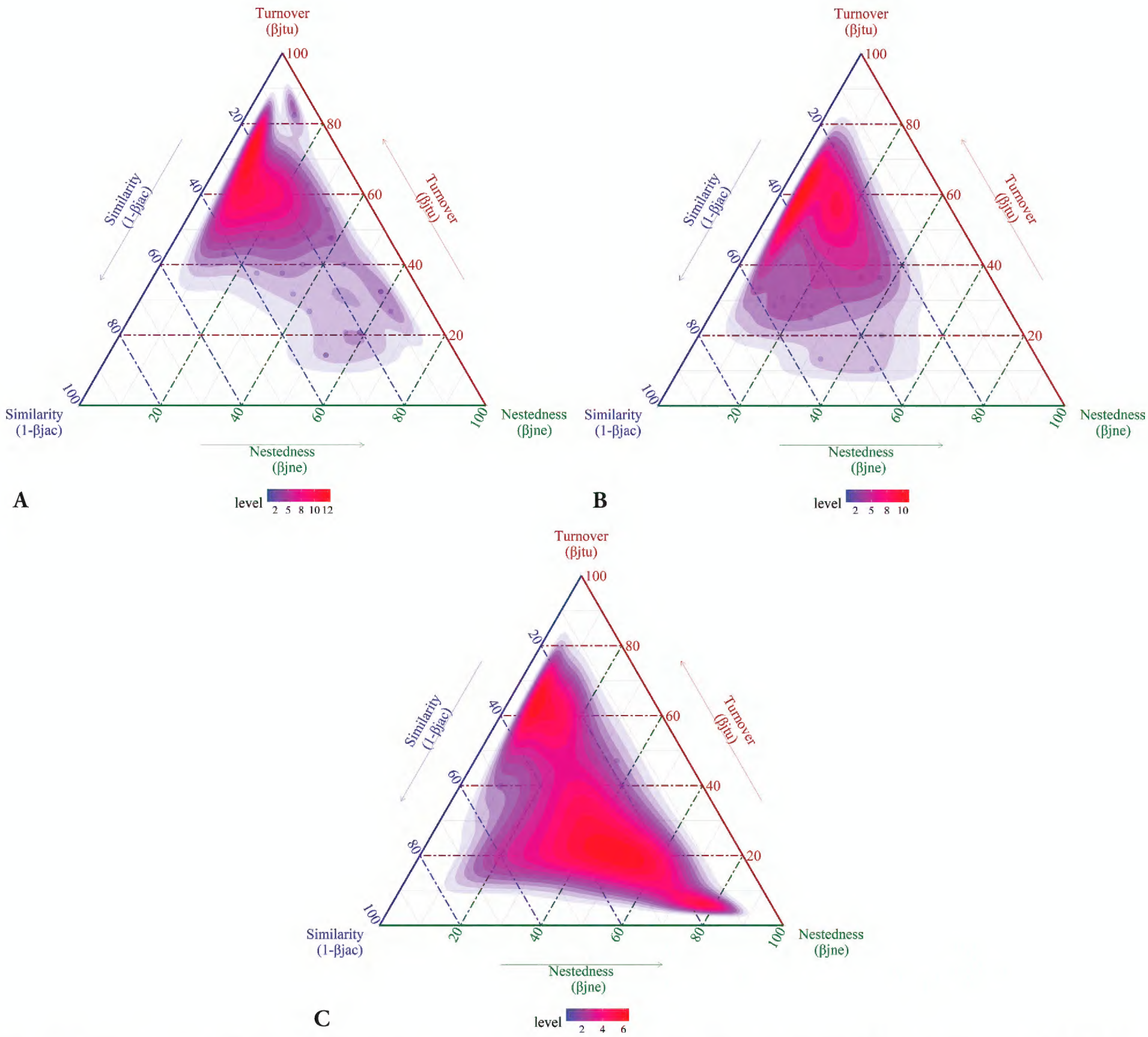

Figure 5. Ternary plots of β diversity decomposition of invasive communities of *P. canaliculata* in the Jianghan Plain. **A.** Paddy fields; **B.** Ditches, and **C.** Lakes.

The middle niche included *P. canaliculata* and *Bellamya* sp., and the narrow niche included *Micronecta* sp., *Diplonychus* sp., *Anisops* sp., *Chironomus* sp., and *P. acuta*. The niche widths of species in ditches ranged from 0.35 to 0.70. The broad niche included *Aciagrion* sp., the middle niche included *Anisops* sp. and *P. acuta*, and the narrow niche included *Micronecta* sp., *P. canaliculata*, *Diplonychus* sp., and *Bellamya* sp. The niche widths of species in lakes ranged from 0.26 to 0.72. The broad niche included *P. canaliculata*, the middle niche included *Bellamya* sp. and *Unio douglasiae*, and other niches were narrow.

Ecological niche overlap

The niche overlap between *P. canaliculata* and the main zoobenthos taxa ranged from 0.22 to 0.89 (Fig. 2). In paddy fields, this niche overlap ranged from 0.22 to 0.42 (Fig. 6A). The overlap between *P. canaliculata* and *Bellamya* sp. was the highest (0.42), followed by that between *P. canaliculata* and

Table 1. Frequency (*fi*), dominance (*Yi*) and ecological niche width (*Bi*) of dominant species.

Number	Species name	Paddy field			Ditches			Lakes		
		fi	***Yi***	***Bi***	***fi***	***Yi***	***Bi***	***fi***	***Yi***	***Bi***
S1	*Chironomus* sp.	0.55	0.04	0.21	–	–	–	–	–	–
S2	*Diplonychus* sp.	0.27	0.02	0.22	0.56	0.02	0.38	0.7	0.03	0.26
S3	*Micronecta* sp.	0.73	0.09	0.35	1	0.06	0.49	–	–	–
S4	*Anisops* sp.	0.55	0.03	0.21	0.89	0.04	0.61	–	–	–
S5	*Aciagrion* sp.	–	–	–	1	0.11	0.70	0.6	0.02	0.34
S6	*Caridina* sp.	–	–	–	0.89	0.09	0.53	0.9	0.18	0.47
S7	*Macrobrachium* sp.	–	–	–	–	–	–	1	0.24	0.31
S8	*Unio douglasiae*	–	–	–	–	–	–	0.6	0.02	0.57
S9	*Physa acuta*	0.55	0.26	0.13	0.67	0.17	0.47	–	–	–
S10	*Pomacea canaliculata*	1	0.27	0.60	1	0.18	0.56	1	0.1	0.72
S11	*Bellamya* sp.	0.91	0.12	0.57	0.78	0.16	0.35	0.9	0.24	0.66

Chironomus sp. (0.37). The overlap between *P. canaliculata* and *Diplonychus* sp., *P. acuta* and *Anisops* sp. was low (O_{ik} < 0.3). In ditches, the niche overlap between *P. canaliculata* and the main zoobenthos taxa ranged from 0.22 to 0.89 (Fig. 6B), with the highest overlap between *P. canaliculata* and *Micronecta* sp. (0.89), followed by that between *P. canaliculata* and *Aciagrion* sp. (0.69). The overlap between *P. acuta* and *P. canaliculata* was low (O_{ik} < 0.3). In lakes, the niche overlap between *P. canaliculata* and the main zoobenthos taxa ranged from 0.25 to 0.83 (Fig. 6C). Species pairs with O_{ik} > 0.6 accounted for 66.7% of the total, with the highest overlap between *P. canaliculata* and *U. douglasiae* (0.83), followed by that between *P. canaliculata* and *Aciagrion* sp. (0.77), *Diplonychus* sp. (0.73), and *Bellamya* sp. (0.6).

Overall, the niche overlap between *P. canaliculata* and the main zoobenthos in lakes was higher than that in ditches and paddy fields. There were 0 pairs with high overlap in paddy fields, 2 in ditches, and 4 in lakes. Overlapping species will engage in intense competition with *P. canaliculata* when resources are scarce. There were 2 pairs with niche overlaps between 0.3 and 0.6 in paddy fields, 3 in ditches, and 1 in lakes, indicating that these species have a certain competitive relationship with *P. canaliculata* but can coexist when resources are abundant. The niche overlap between *P. canaliculata* and the main zoobenthos taxa was low, with 3 pairs in paddy fields, 1 in ditches, and 1 in lakes, indicating that these species have a weak competitive relationship with *P. canaliculata*.

Overall correlation analysis of dominant species

The variance ratios of the overall correlation between dominant species of the invasive community were all > 1 (Table 2), indicating a significant positive correlation between the dominant species communities under the null hypothesis of independence. The *W* statistic indicated that the overall correlation of the dominant species in the paddy fields was significant ($X^2_{0.95} < W < X^2_{0.05}$), and the overall correlation of the dominant species in the ditches and the lakes was not significant. This result indicated that the overall linkage of the dominant species communities in ditches and lakes was relatively loose, and the community structure was more stable than that of the invasive community.

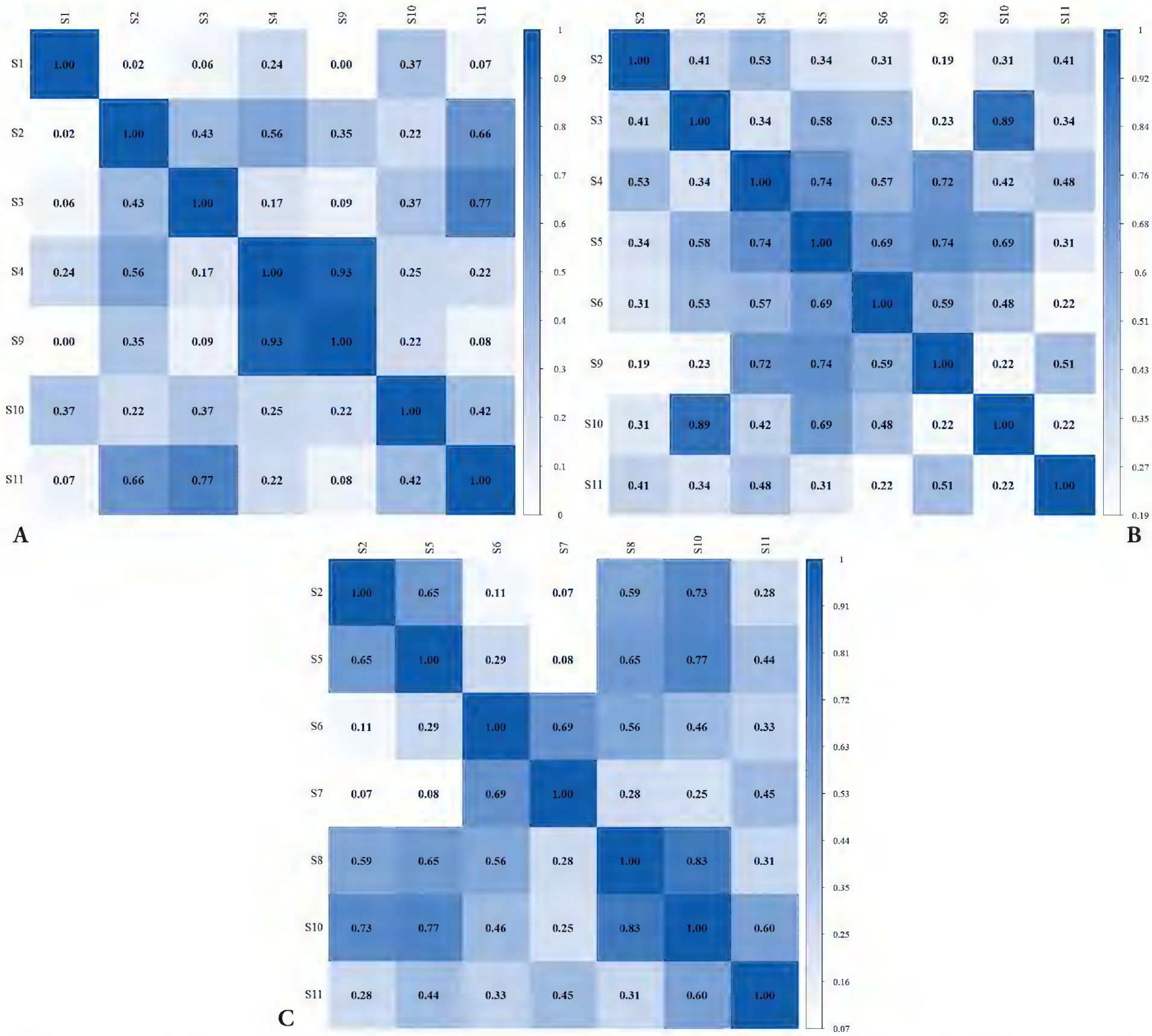

Figure 6. Niche overlap of dominant species in invasive communities. Niche overlap index in **A.** Paddy fields; **B.** Ditches, and **C.** Lakes.

Table 2. Overall correlation of dominant species in invasive communities.

Habitats	Variance ratio	The test statistic *W*	Degrees of freedom *df*	*c* Threshold	Validity results
Paddy field	1.69	18.58	7	[2.18, 14.07]	Significant positive correlation
Ditches	1.53	13.76	8	[2.73, 15.51]	Non-significant positive correlation
Lakes	1.39	13.91	7	[2.18, 14.07]	Non-significant positive correlation
Three habitats	1.51	45.23	11	[4.57, 19.68]	Significant positive correlation

Interspecific associations of dominant species

Among the 55 species pairs (Fig. 7A), 6 pairs had significant associations ($X^2 \geq 3.841$), 3 pairs showed highly significant positive associations ($X^2 > 6.635$, $ad > bc$) (*Micronecta* sp.–*Anisops* sp., *Aciagrion* sp.–*Micronecta* sp., and *P. acuta*–*Anisops* sp., accounting for 5.5% of the total number of pairs), and 1 pair showed highly significant positive associations, accounting for 5.5% of the total number of pairs. One species pair showed a significant positive association ($3.841 \leq X^2 \leq 6.635$, $ad > bc$)

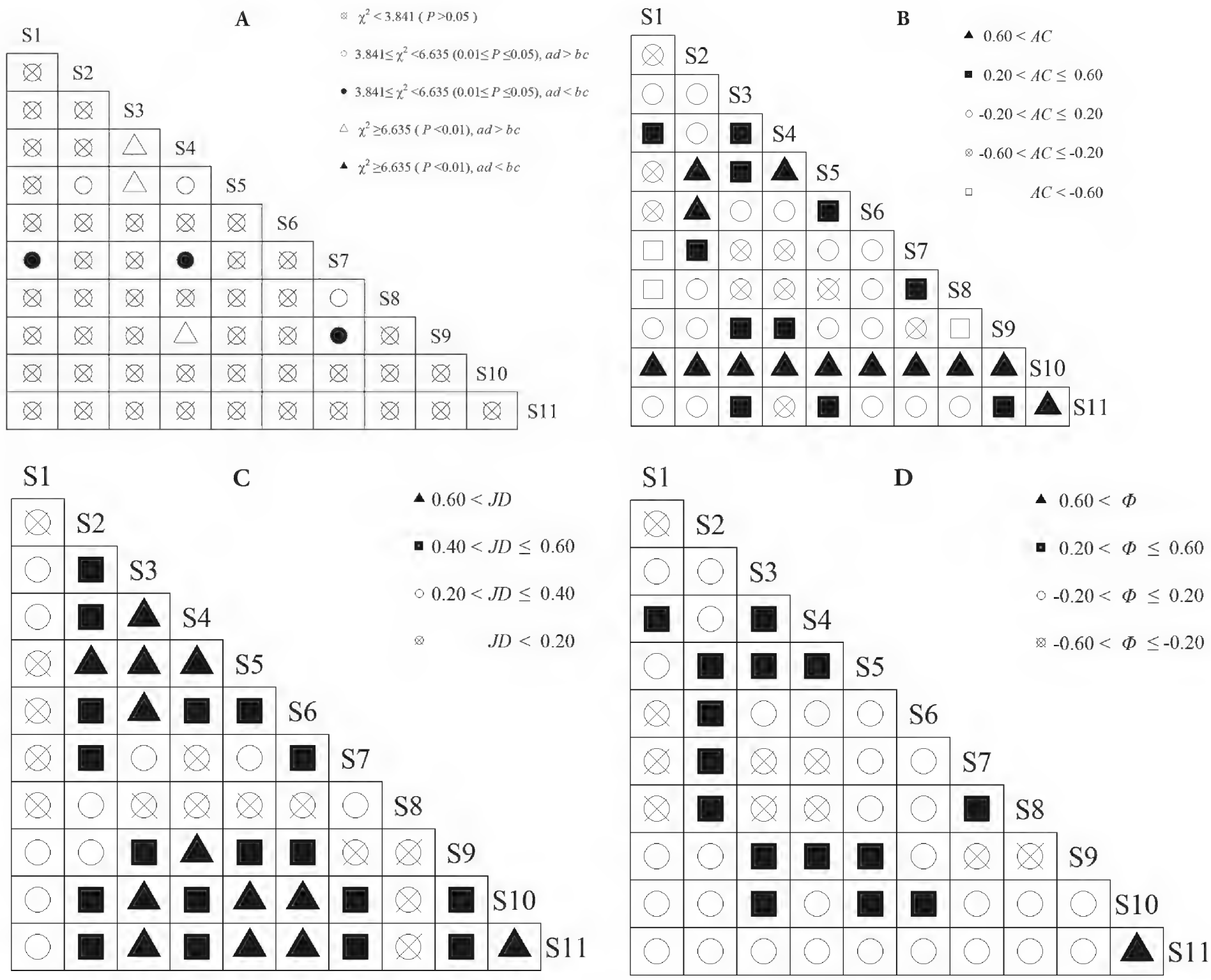

Figure 7. Half-matrix for dominant species. **A.** Half-matrix of X^2; **B.** Half-matrix of coefficients of association (*AC*); **C.** Half-matrix of Jaccard's index; **D.** Half-matrix of point correlation coefficient (Φ).

and forty-six species pairs had non-significant associations, accounting for approximately 83.6% of the total number of species pairs.

The *AC* showed that there were 13 groups of 55 species pairs with a highly significant positive association ($AC \geq 0.60$), accounting for 23.63% of the total number of species pairs; 11 species pairs with a significant positive association ($0.20 \leq AC \leq 0.60$), accounting for 20% of the total number of species pairs; and 3 and 10 species pairs with highly significant ($AC < -0.60$) and significant ($-0.60 \leq AC \leq -0.20$) negative associations, accounting for 5.45% and 18.18% of the total number of species pairs, respectively (Fig. 7B). The high degree of positive associations between *P. canaliculata* and the dominant species in the invasive community indicates that most of the samples were similar in resource utilization at the current stage of succession.

According to the *JD* analysis (Fig. 7C), 13 species pairs had $JD > 0.60$, accounting for 23.63% of the total, whereas 14 species pairs had $JD < 0.20$, which showed no connectivity, and accounted for 25.45% of the total. The association between populations was strong, and the results of *AC* also confirmed this conclusion. *Diplonychus* sp., *Micronecta* sp., *Anisops* sp., *Aciagrion* sp., *Caridina* sp., *Macrobrachium* sp., and *P. canaliculata* were also strongly associated.

The point correlation coefficient (Φ) showed that among 55 species pairs, there were 38 positively linked species pairs, with 1 species pair at $\Phi > 0.6$ showing a stronger positive linkage and accounting for 1.81% of the total number of pairs; 10 species pairs were negatively linked at $-0.2 \leq \Phi < 0.2$, accounting for approximately 18.18% of the total number of pairs (Fig. 7D). There were 29 weak associations, accounting for 52.72% of the total number of pairs. *Micronecta* sp., *Aciagrion* sp., and *Caridina* sp. were strongly associated with *P. canaliculata*, which was consistent with the *JD* results.

Spearman's rank correlation analysis

From the results of Spearman's rank correlation analysis (Fig. 8), there were 29 positively correlated species pairs, accounting for 52.72% of the number of species pairs, of which 6 pairs were significantly positively correlated. There were 26 negatively correlated pairs of species, accounting for 47.28% of the total number of pairs, of which 4 pairs were significantly negatively correlated. Most of the interspecific correlations were not significant, and the interspecific relationships were dominated by positive associations, which was consistent with the *AC* results, indicating that the dominant species were loosely associated with each other, and each of them tended to be independently distributed. *Pomacea canaliculata* was negatively correlated with only *Caridina* sp., *Macrobrachium* sp., and *P. acuta*, and was positively correlated with all other dominant species. Spearman's rank correlation coefficient, which has a higher detection sensitivity, was calculated to show that the association between *P. canaliculata* and *Caridina* sp. was enhanced.

Relationship between environmental factors and species distribution

The Mantel test showed that the biomass and its distribution in the invasive community in paddy fields were significantly affected by NH_3-N ($r = 0.501$). In addition, the invasive community in ditches and its distribution were significantly affected by COD ($r = 0.406$) (Fig. 9), consistent with the overall results.

Redundancy analysis was used, and the Monte Carlo fitting method was applied to test the significance of environmental factors (Fig. 10). The paddy fields were screened for COD, NH_3-N, and TP for analysis, and axes 1 and 2 explained 71.96% and 19.75% of the species variation, respectively, which to a certain extent reflected the relationship between invasive communities and environmental factors and was mainly determined by sorting axis 1. Total phosphorus ($P = 0.033$) and NH_3-N ($P = 0.091$) explained 61.10% and 46.41% of the community variance, respectively, and were the main environmental factors affecting the invasive community in paddy fields (Fig. 10A). *Pomacea canaliculata* (S10) was negatively correlated with NH_3-N.

Ditches were screened for COD, pH, and TN in the RDA. Sorting axes 1 and 2 explained 65.44% and 30.45% of the species variation, respectively, which could reflect the relationship between invasive communities and environmental factors, and was mainly determined by sorting axis 1. Chemical oxygen demand, pH, and TN were the main environmental factors affecting the distribution of species in invasive communities, explaining 92.92%, 79%, and 72.18% of community variation, respectively (Fig. 10B). *Pomacea canaliculata* (S10) showed significant positive correlations with COD and TN.

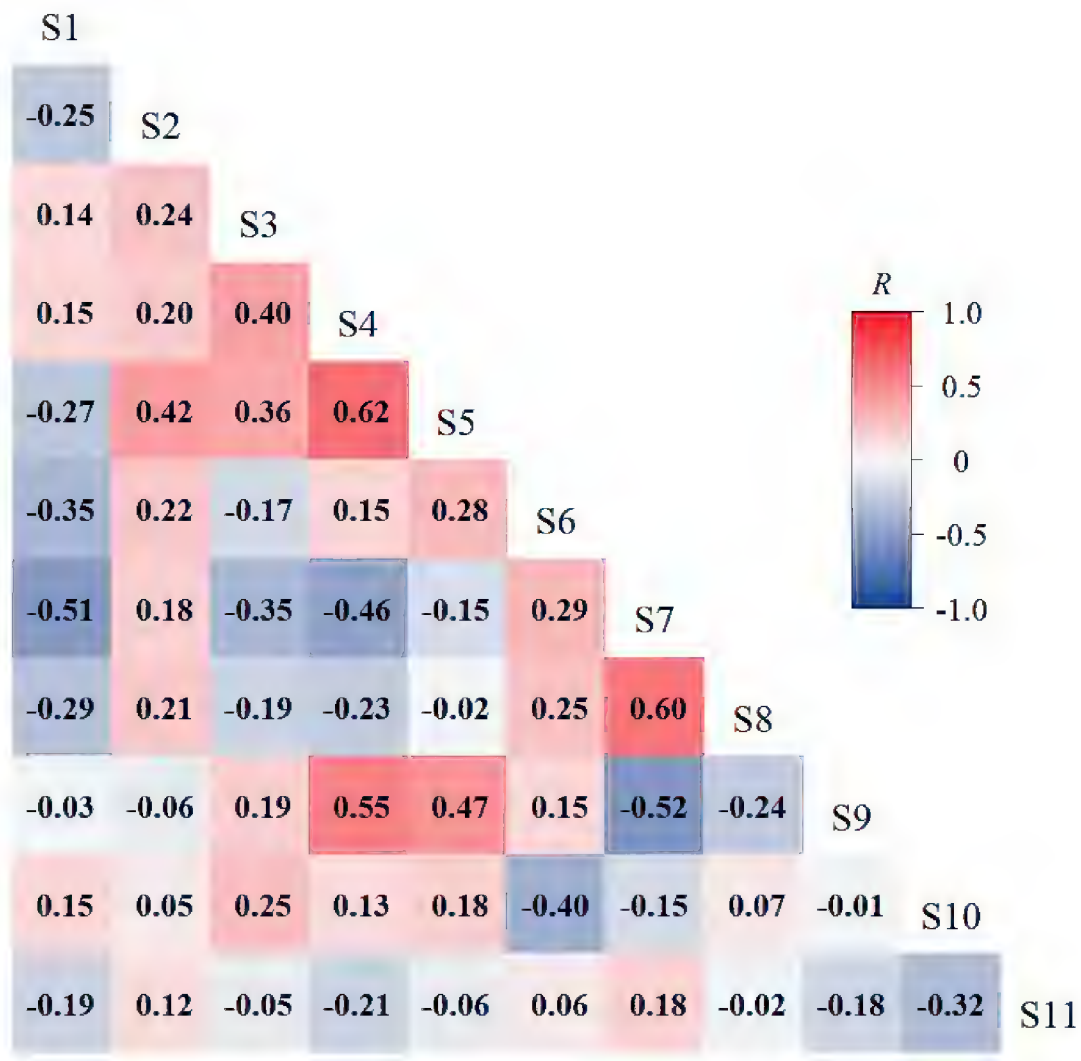

Figure 8. Heat map of interspecific correlation of Spearman's dominant species.

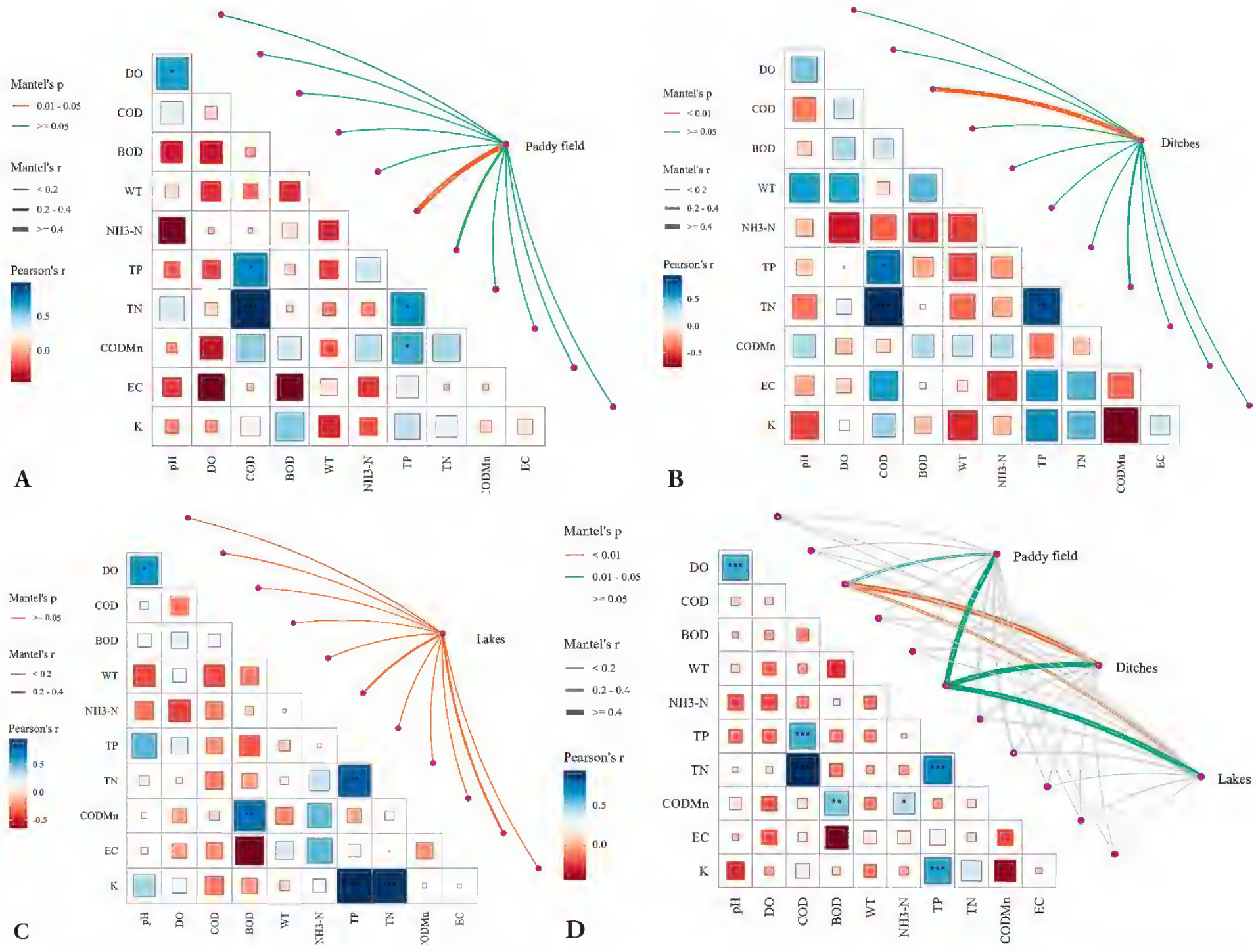

Figure 9. Mantel test results of dominant species and environmental factors in three different habitats of the Jianghan Plain. **A.** Paddy field; **B.** Ditch; **C.** Lakes; **D.** All three habitats.

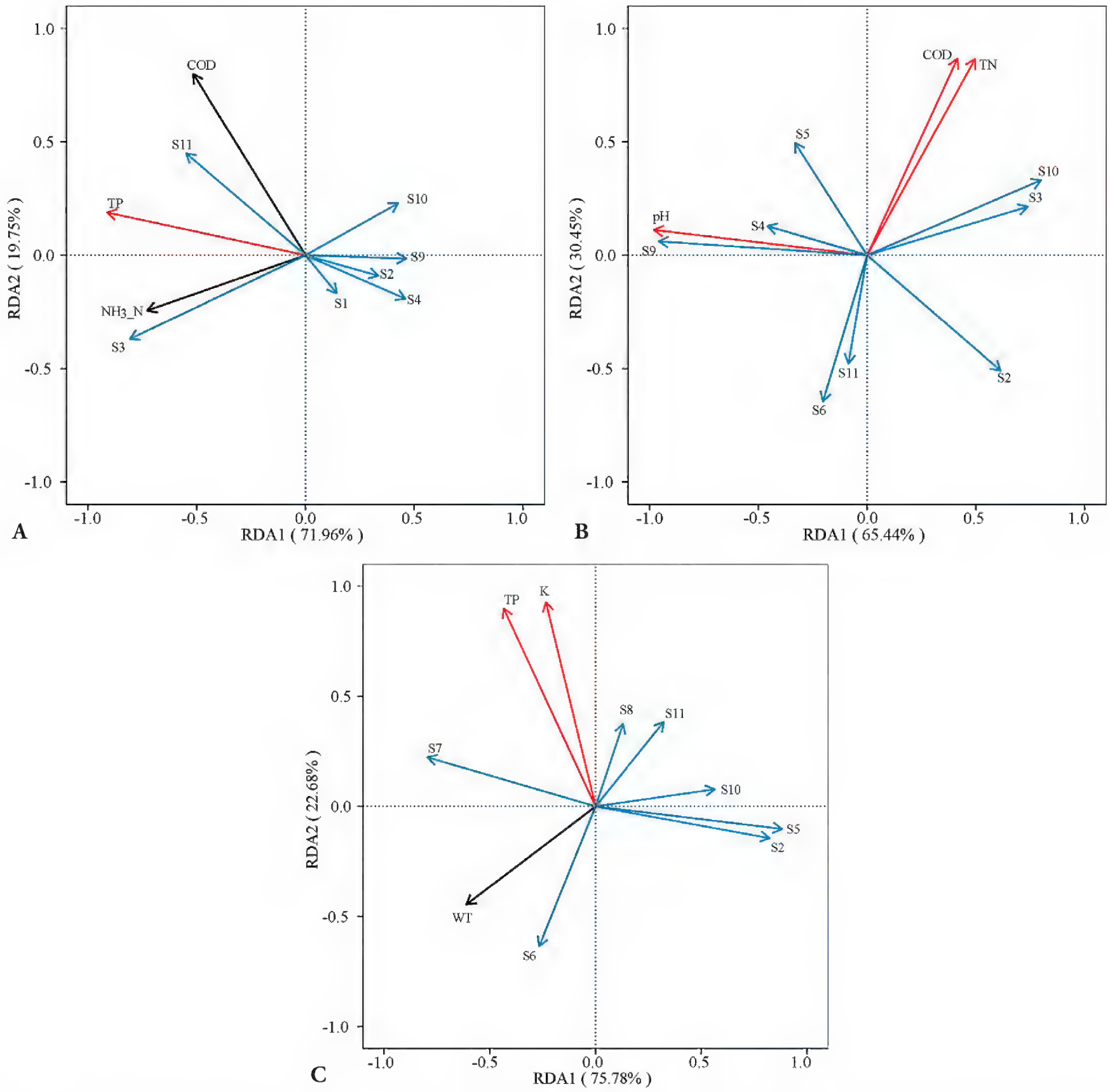

Figure 10. Redundancy analysis of invasive communities. Two-dimensional sorting of dominant species and environment in **A.** Paddy field; **B.** Ditches; **C.** Lakes.

Lakes were screened for TP, K, and WT for analysis, and axes 1 and 2 explained 75.78% and 22.68% of the species variation, respectively, which could reflect the correlation between invasive communities and environmental factors to a greater extent and was mainly determined by sorting axis 1. Total phosphorus (P = 0.011) and K (P = 0.042) explained 83.30% and 73.85% of the variation in invasive communities, respectively (Fig. 10C). *Pomacea canaliculata* (S10) was positively correlated with WT.

Discussion

Ecological niche of the *P. canaliculata* invasive community

Dominance and niche width reflect the status and role of a population within a community (Guo et al. 2021). In the present study, *P. canaliculata* was the dominant species ($Yi \geq 0.1$) with a high niche width (Table 1), indicating its strong competitiveness and ability to adapt to the environment and utilize resources

within the community. Field surveys revealed that *P. canaliculata* are present in most aquatic ecosystems in the Jianghan Plain, indicating their strong adaptability. Combined with their strong reproductive capacity, this is the primary reason for their invasive spread (Wang et al. 2021; Yang et al. 2022; Luo et al. 2023). Among the main zoobenthos species, *Bellamya* sp., *P. acuta*, *Aciagrion* sp., *U. douglasiae*, *Caridina* sp., and *Anisops* sp. occupied larger niche widths, indicating that these species can utilize a broader range of resources (such as food, habitat space, different substrate types, and water depth). During the succession of zoobenthos communities, they can better adapt to environmental changes (Zhao et al. 2024), enabling them to coexist with *P. canaliculata* when resources are abundant. *Diplonychus* sp. and *Micronecta* sp., among other primary zoobenthos species, exhibit a narrower niche width, suggesting specialization in resource utilization (Guo et al. 2021). Their environmental adaptability, resource utilization, and competitive capabilities are relatively weak, placing them at a disadvantage during periods of resource scarcity.

In zoobenthos communities affected by species invasions, overlap in actual niches is commonly observed between native and invasive species, or between species with similar functions (e.g., in food resource utilization or microhabitat selection) (Guo et al. 2021; Zalota et al. 2024). This overlap typically stems from their similar ecological characteristics (e.g., filter-feeding, benthic crawling lifestyle), leading to overlapping demands for resources or environmental conditions (Liu et al. 2021b). Niche overlap can indicate potential interspecific competition. In invaded communities, the degree of overlap may influence invasion success and the survival of native species (Jiang et al. 2019; Guo et al. 2021). Species with wider niches tend to exhibit higher niche overlap (Liu and Cao 2011), and the present study confirmed this view. In lakes (Fig. 7C), *P. canaliculata*, which had the widest niche width, exhibited high niche overlap with most zoobenthos species, revealing its ability as an invasive species to compete with species in that community—including those with narrower niches—for similar habitats and resources. Species pairs with higher niche width, such as *Anisops* sp.,–*Aciagrion* sp., *Aciagrion* sp.–*Caridina* sp., *P. canaliculata*–*Bellamya* sp., *P. canaliculata*–*Aciagrion* sp., and *P. canaliculata*–*U. douglasiae*, exhibited high niche overlap, indicating that these ecologically adaptable benthic organisms share similar life habits or resource requirements and will engage in intense competition as community succession progresses (Xin et al. 2011). The relationship between niches and the niche overlap index is a non-absolute positive correlation influenced by spatial heterogeneity, the existence of differences, or complementary growth requirements (Jiang et al. 2023). Species with broad niches in paddy fields, such as *P. canaliculata*, *Bellamya* sp., and *P. acuta*, exhibited low niche overlap. In contrast, species with narrow niches, such as *Diplonychus* sp. and *Anisops* sp., showed high niche overlap.

Dominant interspecific linkages in *P. canaliculata* invasive communities

The interspecific linkage theory posits that positive linkages occur in two scenarios: (1) one species becomes dependent on another species; and (2) in heterogeneous environments, several species exhibit similar adaptations and responses to the environment but often engage in intense interspecific competition due to resource constraints during the later stages of succession. Negative connections are: (1) species

mutually exclude each other in competing for resources, and (2) dissimilarity in environmental requirements (Xu et al. 2016; Guo et al. 2021; Jiang and Zhang 2021). Generally, as community succession progresses, the composition and structure of the community continue to improve and stabilize, and interspecific relationships tend toward positive associations (Greig-Smith 1983; Zhang 2018). The present study showed that the overall community structure of *P. canaliculata* invasion exhibits significant positive associations (Table 2), and the results of the test, *AC* (Fig. 7B), Φ (Fig. 7D), and Spearman rank correlation coefficient (Fig. 8) indicated that the number of species pairs with positive associations in communities invaded by *P. canaliculata* exceeds the number of species pairs with negative associations. Currently, the structure and function of these communities are undergoing dynamic adjustments. Some species pairs compete for resources such as food and habitat, while most species belong to the second category of positive association, meaning they currently possess the ability to adapt to, and coexist with, one another. However, as the community matures, niche separation and differing growth habits will lead to competitive exclusion between species, which intensifies as resources become scarce (Liu et al. 2021b).

The *JD* and Φ results indicate that *P. canaliculata* exhibits strong ecological connections with *Micronecta* sp., *Aciagrion* sp., *Caridina* sp., and *Bellamya* sp. (Fig. 7). However, in paddy fields, the niche overlap between *P. canaliculata* and *Aciagrion* sp. and *Bellamya* sp. is low (Fig. 6A). It is generally believed that interspecific connectivity is positively correlated with niche overlap indices (Wu et al. 2019), meaning that stronger positive connectivity between species is associated with high niche overlap, and vice versa. However, some studies have suggested that the degree of interspecific association does not consistently correlate with niche overlap (Wu et al. 2019), and similar results were obtained in the present study. This suggests that explaining the interspecific association between *P. canaliculata* and zoobenthos using niche theory has certain limitations. As an invasive species, *P. canaliculata* inevitably competes with other species in the community in terms of resource utilization, and its strong adaptability allows it to deplete environmental resources, which can affect the growth of other species (Zhang et al. 2016). The results of the Spearman rank correlation coefficient test indicate that *P. canaliculata* are positively correlated with *Chironomus* sp., *Diplonychus* sp., *Micronecta* sp., *Anisops* sp., *Aciagrion* sp., and *U. douglasiae* (Fig. 8). This suggests that these species, on the one hand, share similar resource utilization patterns and adaptive responses to environmental changes with *P. canaliculata*, and on the other hand, have strong resistance to *P. canaliculata*. Despite the significant harm caused by *P. canaliculata* to the community, these species are still able to remain in the community. *Caridina* sp., *Macrobrachium* sp., *P. acuta*, and *Bellamya* sp. exhibit a negative correlation with *P. canaliculata* (Fig. 8), indicating a high degree of exclusion, which suggests that these zoobenthos compete with *P. canaliculata* for space, environmental resources, and other factors.

Relationships between environmental factors of dominant species in invasive communities of *P. canaliculata*

Pomacea canaliculata can establish niche advantages by altering aquatic ecological environments, thereby promoting their own expansion while suppressing the growth of native species (Ji et al. 2023). Zoobenthos have complex interactions with their aquatic environments, and moderate concentrations of aquatic environmental factors can have positive effects, whereas excessively high or low concentrations of phys-

icochemical factors in water bodies can have adverse effects (Zhao et al. 2024). In the present study, we used Mantel's tests and RDA to reveal the relationship between *P. canaliculata* and key water environmental factors in different habitats.

In paddy fields, the biomass of *P. canaliculata* was significantly influenced by NH_3-N (P = 0.028) and showed a negative correlation (Fig. 9A). The extensive feeding of *P. canaliculata* leads to the excretion of large amounts of secretions and excreta, increasing NH_3-N levels in the water. However, excessively high NH_3-N concentrations in the water are detrimental to the development of juvenile snails (Pan et al. 2014). Additionally, frequent agricultural activities in paddy fields (such as drying fields and draining water) directly inhibit the growth of snail populations.

In ditches, the biomass of *P. canaliculata* was significantly influenced by COD (P = 0.008) and showed a significant positive correlation with COD and TN (Fig. 9B). *Pomacea canaliculata* exhibit strong tolerance to polluted water, and water pollution does not serve as a lethal ecological factor for them (Andrews 1965; Yang and Feng 2006). Turbid water quality is generally associated with low DO levels. *Pomacea canaliculata* possess two respiratory systems: in clean water with high DO levels, they can breathe using their gills; in turbid water with low DO levels, they often climb onto aquatic plants and rocks or float on the water surface, extending their respiratory tubes to breathe using their lungs (Andrews 2010; Pan et al. 2014). Conversely, native snails are highly sensitive to water quality and DO levels (Yang and Feng 2006). Additionally, the discharge of nitrogen-rich wastewater from farmland increases total nitrogen levels in ditches, promoting the growth of submerged plants and algae, which indirectly provide abundant food resources and habitats for *P. canaliculata* (Luo et al. 2023).

In lakes, the biomass of *P. canaliculata* was primarily influenced by WT. *Pomacea canaliculata* have a wide temperature ecological range, and low temperatures often become the limiting ecological factor for their population expansion compared to high temperatures (Bae and Park 2015; Yang et al. 2022). Our field surveys indicate that lakes in the Jianghan Plain are less affected by human factors, with WT emerging as the dominant natural factor influencing snail distribution. Water quality monitoring confirmed that increased WT (within the optimal range) promotes snail population growth.

In this study, *P. canaliculata* triggered a "biotic-environmental" positive feedback loop based on the associated increase in NH_3-N and TP in the aquatic environment. The elevated concentrations of NH_3-N and TP in the aquatic environment may be the result of the combined effect of large-scale agricultural effluent discharge and *P. canaliculata* invasion in the Jianghan Plain. Specifically, the application of fertilizers and feeds associated with large-scale rice-shrimp co-culture farming has intensified eutrophication. Meanwhile, the excretions and benthic disturbances caused by *P. canaliculata* have directly contributed to increased levels of NH_3-N and TP in the water. This has promoted the growth of pollution-tolerant plants (e.g., *Alternanthera philoxeroides* and *Myriophyllum aquaticum*) and provided habitats and food resources to further expand the snail populations.

Food resources are the primary factor influencing the composition of functional feeding groups in benthic organisms, so the composition of these groups can reflect the status of food resources in different habitats. In the three different habitats studied, the dominant groups were predators and scrapers, while filter feeders, collectors, and shredders were less common. This phenomenon may be attributed to human disturbances. As the habitat type transitions from lakes to ditches and then to paddy fields,

the gradual increase in agricultural production leads to slower or stagnant water flow, and the substrate changes from sediment to muddy, providing abundant food resources for predators and scrapers, making it suitable for their growth. Due to the impact of agricultural wastewater discharge, there is a lack of external organic debris input, resulting in fewer fine organic particles, which significantly reduces the proportion of filter feeders, collectors, and shredders. Paddy fields, ditches, and lakes provide food resources and serve as excellent habitats for *P. canaliculata*, enabling its widespread distribution across the Jianghan Plain and ultimately altering the benthic community structure.

Conclusion

The following results were obtained.

1. The dominance of *P. canaliculata* was highest in paddy fields and ditches (paddy fields Y_i = 0.27, ditches Y_i = 0.18), whereas *Macrobrachium* sp. was dominant in lakes (Y_i = 0.24). The niche width of *P. canaliculata* was largest in paddy fields and lakes, whereas that of *Aciagrion* sp. was largest in ditches. The niche overlap of *P. canaliculata* in lakes and ditches was relatively high, with average values of 0.61 and 0.54, respectively, while the niche overlap of *P. canaliculata* in paddy fields was relatively low, with average values of 0.31.
2. The overall connectivity and interspecific connectivity of dominant species in invasive communities exhibit positive correlations in all three habitats, indicating that the communities are in a stable state. *Pomacea canaliculata* was closely associated with *Diplonychus* sp., *Micronecta* sp., *Anisops* sp., *Aciagrion* sp., *Caridina* sp., and *Macrobrachium* sp., indicating that *P. canaliculata* shares similar resource utilization patterns with these species.
3. The environmental factors significantly influencing the composition of the dominant species in the invasive community of *P. canaliculata* are TN, COD, NH_3-N and WT.
4. As China's bread basket, the agricultural output of the Jianghan Plain is crucial to global food security. This study provides a scientific basis for regional control measures by analyzing the invasion mechanisms of *P. canaliculata*: in paddy fields and ditches, dynamic monitoring of population density is required; in lakes, human interference should be reduced to maintain ecological balance.

This study provides an initial overview of the niche and interspecific relationships of *P. canaliculata* in the Jianghan Plain. To gain a detailed understanding of the succession of invasive communities in this region, long-term monitoring is required. In subsequent studies, the temporal and spatial scales of research will be expanded, thereby enabling a more comprehensive assessment of the ecological effects of *P. canaliculata* invasion.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

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Author contributions

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Data availability

Yu Zhou, Jing Xue, and Zhaohua Li were responsible for the overall design of the study and contributed to proofreading the manuscript; Yu Zhou performed the experiments, interpreted the data, and wrote and proofread the manuscript; Yu Zhou, Jinghua Wang, Jing Xue, Guodong Zhang, Hui Li, and Shaoping Zhu participated in the field investigation; Zhaohua Li, Jing Xue, Dan Fan, and Haiping Feng designed the study and proofread the manuscript. All authors have read and approved the final manuscript.

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Supplementary material 1

Survey and sampling site selection of *Pomacea canaliculata*

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Supplementary material 2

Additional information

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Supplementary material 3

List of zoobenthos

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